

NOTES ON THE METHODS OF FERTILISATION OF THE *GOODENIACEÆ*.

PART II.

BY ALEX. G. HAMILTON.

(Plate xxiv.)

The interesting genus *Dampiera* is entirely Australian, and is remarkably distinct and easily determined.

The calyx-tube is adnate to the ovulary, which is in nearly every case 1-celled. The corolla-tube is deeply slit; the two upper lobes stand well above the lower three, and are closely pressed together, the posterior margins folding in between the lobes, and forming a cavity or auricle which encloses the style and indusium, and which is of various degrees of complexity in different species. The auricle may be taken as characteristic of the genus, for although it is found in *Goodenia*, *Vellea*, and *Anthotium*, yet in its highest development in those genera, it does not approach the simplest form in *Dampiera* as regards completeness of structure. The anterior margins of the upper lobe also fold under into the tube of the corolla, projecting in such a manner as to cause the auricles to separate when an insect forces its way into the tube. The three lower lobes are spreading and usually broadly winged; at their base the wings are narrower and puckered up by the close approach of the lobes, forming guiding lines to the nectar. The throat is always glabrous and free from hairs. The anthers are connate round the style, although in very young buds they are sometimes free, but the growth of the anthers locks them together later on. The style is always glabrous, and often deeply coloured; the indusium is never hairy on the outside as in every other genus except *Brunonia* (and even in this there are hairs in the early

stages, which are deciduous), and rarely ciliate on the lip. The lip of the indusium is shallow, and usually divided into two, or sometimes four, by notches. The indusium and stigma are in most species of a very dark colour. The stigma rarely grows out to project beyond the indusium lips, which is also the case in other plants of the order. The plants, with the exception of *D. diversifolia*, De Vr., are always clothed with silky, cottony, woolly, stellate or branching hairs on the calyx, and the outside of the corolla (except the wings) and sometimes on the stems and leaves. The flowers are almost always blue or purple. In the remarks on the genus in *Flora Australiensis* [1] the colour is said to be blue, purple, red, white, or rarely yellow. This latter colour I have not seen in any fresh specimens (except in the tube), and in dried plants it is very difficult to make out the colour. But from an analysis of the descriptions in *Flora Australiensis*, it appears that of the 34 species described, 23 are blue or purple, 1 white, and 1 (*D. rosmarinifolia*, Schl.) is said to be white, blue or red; while 9 have no colour mentioned.

The characteristic features by which they may be recognised are the solitary ovules, connate anthers, the auricles, and the hairless style and indusium.

From their dense covering of hairs they have the aspect of desert plants, and judging by the number of species collected by the Elder Expedition, they are plentiful in the arid interior of Australia as compared with other genera of the order. And many of the species of other genera occurring there are also tomentose. The Census of Australian Plants [2] gives in all 38 species of the genus, which are distributed as follows:—West Australia has 29 species, 26 of which are endemic; South Australia 5 species, none endemic (this number would probably be much higher were the central parts of the colony collected over); Victoria has 5 species, none endemic; Tasmania has 1 species found elsewhere also; New South Wales has 7 species, 1 being confined to the colony; Queensland has 6 species, 2 endemic; and North Australia 1 species, occurring elsewhere also. From this it will be seen that the head-quarters of the genus is in West

Australia, and a close examination of all the species there would doubtless reveal some interesting indications of the line of evolution. One or two such facts came under my notice in working out some species from that colony.

I have to thank Mr. C. Moore, F.L.S., Director of the Botanical Gardens, and Mr. C. T. Musson, F.L.S., for specimens of several New South Wales *Dampieras* and other Goodeniads, and through the kindness of Mr. J. H. Maiden, F.L.S., Director of Technical Education, and Mr. J. J. Fletcher, I have been enabled to see and analyse the species of *Dampiera* collected by the Elder Expedition, and presented to the herbaria of the Technological Museum and the Linnean Society. It is these and some fresh New South Wales species that I propose to treat of in the following notes.

1. DAMPIERA BROWNII, F.V.M.

In the young buds the stigma is button-shaped, no indusium being visible, but a slight fosse shows across the top (Fig. 1). In the next stage the indusium shows as a thin wall of irregular height all round, but with a notch at each end, and at right angles to the line of the stigmatic groove. During these stages the whole pistil is green. At the next stage the indusium is grown up level all round (Fig. 2), except at the notches, and both indusium and stigma are coloured deep purple, but the style remains green; the purple colour appears first on the stigma, and spreads afterwards to the indusium. The style still continues to elongate and passes into the auricle, the top of the style bending over so as to bring the opening over the junction of the two auricles. During this period the indusium closes by the opposite segments (divided by the notches) approaching, and at last there is only a small circular opening. The indusium has been packed with pollen by growing up through the anthers while the mouth was wide open, and when the stigma begins its outgrowth at this period it forces the pollen out in a small worm-like string, which when exposed to the air falls in powder into the auricles, where it lies. An insect forcing its way into the tube of the flower presses

against the fold of the anterior margin and so moves the auricles apart, when the pollen falls in a small shower on its thorax and head. All these contrivances point towards insect-fertilisation, but to complete the process one would imagine that the stigma should now grow beyond the lips of the indusium and project as has been described in *Scavola* and *Selliera* [5]. But in at least ninety-five per cent. of the flowers the stigma does not project at all beyond the mouth, and in many it does not grow up to the level. Examination of large numbers of flowers just withering showed the outside of the indusium, the stigma, and between the stigma and the inner side of the walls of the indusium coated evenly with pollen all over, and this was apparently caused by the close fit of the auricles round the style applying the pollen, and not by insect agency at all. I can only conjecture that the plant is ordinarily self-fertilised, although occasionally cross-fertilisation may occur from insect visits when the stigma is outgrown or near the mouth of the indusium. From the firmness of the hold which the auricles have upon the style, any insect would, in forcing its way in, press hard against the style and might thus deposit pollen upon the stigma, even though it was only at the mouth of the indusium, instead of projecting as in other genera. It is usual to find the auricles full of pollen where the flower and even the style is withered, so that insects do not commonly exhaust the pollen. The flowers are very sweetly scented, and there is a considerable amount of moisture at the base of the petals, in which, however, I could not detect any sweetness. As already pointed out, the membranous edges of the three lower petals are closely pressed together in the tube, and pucker so as to form guiding ridges (Fig. 3). The flowers are much frequented by Thrips. The auricles in the early bud are green, without any deep concavity, and with a pale red spot where the deepest colour occurs in the mature flower; this is indicated by the dotted oval in Fig. 4, which represents a young auricle. In this stage it resembles the mature auricle in *D. linearis* (Fig. 12). It gradually darkens till it is a fine purple-red with the central part a purple-black of wonderful intensity. This bears out Dr. A. R. Wallace's

theory that the parts of an organism that have undergone the most modification also show the greatest depth of colouring. The flower-stalks and undersides of the leaves are densely covered with stellate hairs; the upper-sides of the leaves are less thickly covered, and the edges are armed with short thick conical hairs. The calyx and lobes of corolla (but not the membranous wings) are covered with dark olive-green branching hairs, resembling those of *D. luteiflora* (Fig. 14).

Referring to this genus, Mr. Bentham says [3]: "In *Dampiera* the summit of the style, when short in the buds, has the appearance of an ordinary peltate stigma, except that it is not yet papillose, flat and nearly circular, with the rudiment of the stigma across the centre. It soon rises, the margins are raised into a short almost two-lipped indusium; but I do not find that it carries any pollen with it, and the stigma does not assume the perfect appearance till the whole indusium and the stigma has ensconced itself between the two upper petals, which closely embrace it by means of two thickened concave appendages, requiring some external agency to open them and give access to the pollen."

This is a perfectly accurate description of the mechanism of the flower, except that the pollen is carried by the up-growing style. Indeed, in reading the paper I was struck with the correctness of the descriptions of the process in all the genera; and it is all the more remarkable when it is remembered that the author had only dried plants to deal with.

After finishing the above account of *D. Brownii*, I observed a fact which I had previously missed, but which is of great importance. A very large proportion of the flowers of this species are resupinate, so that the auricles are on the lower side and the three other petals on the upper side of the flower. When a flower is in this position it is manifestly impossible for the pollen accumulated in the auricles to drop out on the insect. But on the other hand, an insect visiting such a flower would be smeared on the underside by the projecting stream of pollen coming out of the indusium, and in visiting another flower in which all the pollen had been exuded the pollen from other flowers would be left on

the indusium and would so have a chance of reaching the stigma, even if that organ did not grow out. It is remarkable, however, that in the same plant some flowers should be resupinate and others in the ordinary position. So far as I know of the other genera only *Leschenaultia* has resupinate flowers.

2. DAMPIERA STRICTA, R.Br.

This species on the whole resembles *D. Brownii* in its mechanism, but with some minor differences. It grows in patches in swampy ground, and flowers very freely, so that the masses are very conspicuous. The colour is bright blue with a yellow eye. The indusium has four notches (Fig. 6), and closes more completely than in the last species (Fig. 7); the edges are not even, but slightly ragged, and the shoulder of the indusium is papillose, as shown in the figure. The auricles resemble those of *D. Brownii*, but have a fringe of sticky crimson hairs along the posterior margin (Fig. 8) which are generally longer on the left-hand lobe (looking from behind the flower). In this it resembles *D. eriocephala*. Guiding ridges are present in the tube of the corolla, which is yellowish. The stem, calyx and centre of the outside of the corolla-lobes are hairy, the hairs being either stellate or branching. In the latter case they are very curious in form (Fig. 9). I am at a loss to imagine what can be the function of the trichomes on the edge of the margin, unless they are to exclude small creeping insects, or to prevent moisture from gaining access to the pollen, as mentioned later on. They certainly do not keep Thrips out. The stigma rarely grows out level with the mouth of the cup; the auricles are usually full of powdery pollen, and the style and indusium evenly coated with it. The flowers spread out in a horizontal plane. The process of fertilisation is as in the last species so far as I can see—that is to say, usually self-fertilisation obtains.

3. DAMPIERA LINEARIS, R.Br.

Of this species I have examined only dried specimens. The calyx and corolla are covered with hairs resembling those of *D.*

luteiflora. The indusium is not two-lipped but continuous all round, and shows an approach to ciliation (Fig. 11). The stigma, in perfect flowers, is very near the mouth as shown in the figure. As I had flowers only to examine, I do not know how it is placed in the bud. The auricle (Fig. 12) shows little differentiation, the wing which forms it being merely folded inwards, and slightly hollowed for the reception of the indusium. It is not coloured. In the imperfect ciliation, it forms a link between *Sccevola* and *Goodenia* on the one hand, and the more complicated arrangements of the typical *Dampieras* on the other. The margin indeed resembles that of *Sccevola ovalifolia* in early bud, where the cilia at first exist as a thin membrane continuous all round the indusium, which afterwards breaks up into separate cilia. The plant is obviously well adapted for insect-fertilisation, as a pollen-coated insect, pressing into the tube, could scarcely fail to leave pollen on the stigma.

4. DAMPIERA sp?

An unnamed species from Yeodamie, W.A., in the Technological Museum Herbarium, has the auricle more developed (Fig. 13) and coloured, but not deeply; the indusium also is pale in tint, and, as in *D. linearis*, there is an approach to ciliation of the margin of the indusium. This species is closely covered with cottony hairs. Like the last, it is probably insect-fertilised.

5. DAMPIERA LUTEIFLORA, F.v.M.

I have seen only dried specimens. The calyx, corolla and stems are thickly covered with yellow hairs, mostly branching (Fig. 14). The indusium is very short and two-lipped (Fig. 16). I did not see an outgrown stigma, or even one level with the mouth, but the amount of material at my disposal was so small that it cannot be said certainly that it does not do so. But from the shallowness of the indusium, this would be a matter of less importance, and would not, as in some other species, be any impediment to the deposit of pollen on the stigma by insect agency. The shoulder of the indusium is papillose as in *D. stricta*. The auricle (Fig. 15) is rather simple. The indusium is invariably full of pollen, and it is present also in the auricles.

6. DAMPIERA LINSCHOTENII, F.v.M.

Dried specimens only were examined. The plant is hairy on the calyx and corolla, the hairs being branched. The indusium is markedly two-lipped (Fig. 20), deep, and full of pollen. The stigma in the one flower I had for examination was not outgrown. The indusium is deeply coloured, and the colour runs down the style a short distance. The auricles (Fig. 21) are deeply coloured, and are considerably differentiated. This species, therefore, falls in the group like *D. Brownii*, the members of which are not perfectly adapted to insect visitors.

7. DAMPIERA ERIOCEPHALA, De Vr.

I have seen only dried specimens of this species. The plant is remarkably hairy, being clothed, even on the leaves, with long silky hairs, which are all simple, and usually pure white. The tube of the corolla is bright yellow, and has guiding ridges. The auricles are well developed (Fig. 19), and deep purple in colour. They have trichomes (Fig. 18) on the posterior margin, as in *D. stricta*. These are felted together at their bases, and there are deep crimson, the free extremities being pink. Outside of these the long silky hairs of the calyx are tangled together. The indusium is dark coloured, but the style below is yellow. The remarkable feature is that the indusium consists of very short cilia, so that the stigma is exposed to the touch of any insect forcing the auricles apart. From this circumstance it is very well adapted for insect-fertilisation, resembling *D. linearis* and *D. luteiflora* in this respect. I found all the stigmas I examined coated with pollen, though none showed any outgrowth. But from the small amount of material I had it would not be safe to infer that it does not grow out.

8. DAMPIERA LORANTHIFOLIA, F.v.M.

I have seen dried specimens only. The calyx and exterior of the corolla are thickly coated with white hairs. The petals form ridges in the tube. The auricles are very complex, and very rich

crimson. The indusium is deep, two-lipped and dark red. The stigma was not outgrown in any flowers I had, and pollen was present in every instance.

9. DAMPIERA JUNCEA, Benth.

I have seen only a dried specimen, which was hairy all over, although in *Flora Australiensis* it is described as "glabrous except the flowers or the young shoots, white tomentose." In the one flower which I have had an opportunity of seeing the corolla was missing, but it is described by Bentham as rather large. The indusium was remarkable for its small size, being little greater in diameter than the style; the stigma was outgrown in a crescent. Neither indusium nor style was coloured. From the outgrowth of the stigma, it is evidently adapted for fertilisation by insects. But it is scarcely safe to infer that the stigma is always outgrown, as, in even *D. Brownii*, it sometimes does so, and in this instance it might be an exceptional case which presented itself.

10. DAMPIERA ADPRESSA, A. Cunn.

Covered with long silvery hairs in all parts; these, however, disappear from the leaves as they grow older. The auricles are well developed. The indusium is deep, and two-lipped. The lips flatten over the stigma when the cup is filled with pollen. No outgrowth was seen in any flowers examined. This appears to fall within the group in which self-fertilisation occurs more usually than cross-fertilisation.

11. DAMPIERA LANCEOLATA, A. Cunn.

The plant is hairy, the hairs on the calyx and exterior of the corolla being branched. The corolla is purple, the tube being yellow, and this colour extends to the wider part of the petals so that there is a very decided eye. The margins of the petals in the tube are ridged to form guiding lines. The auricles are well developed, resembling those of *D. stricta*, and, as in that species, there are trichomes on the posterior margins, which are not,

however, deeply coloured. The colour is very deep purple. The indusium is two-lipped, and in mature flowers closes, except for a small central opening. In all the older flowers I examined the indusium was full of pollen, and the auricles lined with a sheet of adhering grains. The indusium and stigma are purple, the style below green. In no instance did I see the stigma outgrown, or even so near the opening as to be capable of receiving pollen from a visiting insect, so that this species also falls within the group not fully adapted for insect-fertilisation; this is therefore another species with arrangements for fertilisation complete except at one point.

Summing up, it appears that in *Dampiera* there is a complex mechanism directed towards the accomplishment of cross-fertilisation by insects, and yet most species examined stop short of completeness, from the stigma's not growing out so as to be exposed to the touch of pollen-laden visitors. Those examined may be divided into two groups; those having either a shallow indusium so that the stigma may be reached by insects; and those in which the indusium is deep, and from the stigma's not growing out, incapable of being insect-fertilised. In the first of these groups are *D. linearis*, sp. (?), *eriocephala* and *juncea*; in the latter *D. Brownii*, *stricta*, *luteiflora*, *Linschotenii*, *loranthifolia*, *lanceolata*, and *adpressa*.

The various species I have examined show a gradation in the completeness of adaptation of the various parts. Thus in the auricles there is a progression from the simple fold with a slight hollow in the centre (*D. linearis*) to the most complex arrangement of folds, hairs and trichomes as in *D. stricta* and *D. Brownii*. And in those species which show this gradual increase of adaptation, there is also a regular augmentation of colour in the auricles, from the simplest with a patch of faint colour in the centre, to the deep purple spread all over the auricle in the most complex forms. This is also the case in the style, which varies from green to purple, and the indusium, from pale red to purple. The stigma is always coloured, in which the genus differs from almost every other member of the order. The indusium also varies from the

shallow and simple ring of cilia to the perfectly closed and protected cup in *D. Brownii*, or *D. stricta*. This makes the fact that the simplest and most open indusium (which may be looked upon as the ancestral form of the genus or near it) is the more remarkable, as it is best adapted for pollination by insects.

Grant Allen points out [4] that a high development of flower usually goes with a reduction of the number of carpels or seeds, because the plant is certain to be fertilised and so the seeds more likely to arrive at maturity. This theory would appear to be supported by *Dampiera*. The theory, strongly advocated by the same author, that blue denotes the highest development in a family, agrees well with the facts. *Dampiera* is certainly one of the highest developed, if not the very highest, of the order, and as already pointed out blues and purples prevail in the genus. The auricles, too, which are the most highly differentiated organs, show the greatest depth of colour, and as this colour is hidden from insects and cannot be intended as an attraction, I think it may be fairly inferred that it is a concomitant of the high development. It is significant that the indusium, and the auricles, when present, in other members of the order, often show deep tints of brown, red, and purple.

The pollen of all the species examined was small, round, and after exposure to the air, dusty, and so is well adapted for falling from the auricles in a shower on a visitor.

The genus, I think, gives a clue to the purpose of the hairs on the style, and the exterior of the indusium (not the cilia, which have a well defined function as pointed out in a previous paper [5]) in the plants of the Goodeniaceæ. They occur in *Velleia*, *Goodenia*, *Scævola*, *Selliera*, *Leschenaultia*, and, slightly, in *Brunonia*. Now in all these the style is wholly (or in those species with auricles, partly) exposed to the air, rain and dew. But the drops collecting in the flower are prevented by the hairs from reaching the indusium and thus damaging the pollen, or clogging it so that it could no longer fall freely. Even in those which have auricles, rain falling on the style would run along to the indusium but for the hairs. But in *Dampiera* only, the whole

style and indusium is closely—very closely—boxed up between the auricles, and the line of junction covered by a closely pressed clothing of hairs. It is possible that the trichomes on the posterior margins of the auricles of *D. stricta*, *D. eriocephala*, and *D. lanceolata* subserve the same purpose. At any rate, I think that the hairy styles occurring in flowers which are open to rain, &c., and the glabrous ones in those which are perfectly protected, is something more than a coincidence.

REFERENCES TO LITERATURE.

- (1) BENTHAM and MUELLER. Flora Australiensis, Vol. iv. p. 106.
- (2) MUELLER, F.v. Second Systematic Census of Australian Plants, p. 146.
- (3) BENTHAM, G. "Note on the Stigmatic Apparatus of *Goode-noria*," Journ. Linn. Soc. Botany, Vol. x. p. 205.
- (4) ALLEN, GRANT. "Colours of Flowers," Nature Series, 1882, pp. 38 and 39.
- (5) HAMILTON, A. G. "Notes on Methods of Fertilisation of *Goodeniaceæ*," Part I. P.L.S.N.S.W. (2), Vol. ix. p. 201.

EXPLANATION OF PLATE.

Dampiera Brownii, F.v.M.

- Fig. 1.—Top of style in early bud; *a*, from above.
 Fig. 2.—Indusium when fully developed.
 Fig. 3.—Guiding ridges in corolla.
 Fig. 4.—Young auricle.
 Fig. 5.—Mature auricle.

Dampiera stricta, R.Br.

- Fig. 6.—Indusium open, from above.
 Fig. 7.—Indusium closed, side view.
 Fig. 8.—Trichomes on edge of auricles.
 Fig. 9.—Calyx hairs.
 Fig. 10.—Auricles, showing trichomes.

Dampiera linearis, R.Br.

Fig. 11.—Indusium showing stigma.

Fig. 12.—Auricle.

Dampiera sp. (?)

Fig. 13.—Auricle.

Dampiera luteiflora, F.v.M.

Fig. 14.—Hairs from calyx.

Fig. 15.—Auricle.

Fig. 16.—Indusium.

Dampiera eriocephala, De Vr.

Fig. 17.—Indusium.

Fig. 18.—Trichomes.

Fig. 19.—Auricle.

Dampiera Linschotenii, F.v.M.

Fig. 20.—Auricle.

Fig. 21.—Top of indusium.

ON A FOSSIL MAMMAL ALLIED TO *HYPSIPRYMNUS*,
BUT RESEMBLING IN SOME POINTS THE
PLAGIAULACIDÆ.

By ROBERT BROOM, B.Sc., M.B., C.M.*

(Plate xxv.)

* This paper, by permission of the Council, has been withdrawn, to allow of the incorporation of observations on some important, and in some respects more perfect, material discovered shortly after it was read. The new paper will appear in a later Part of this Volume. Plate xxv., in illustration thereof, is held over for the present.—ED.